REPRODUCTIVE ECOLOGY OF NEW ZEALAND FORESTS: 1. NATURAL SEED STORAGE PHENOMENA

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ABSTRACT

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A brief survey of the subject area of natural seed storage is followed by a summary of New Zealand research on this topic in relation to native forests. Examples of seed storage periods from published studies indicate that different species can store "ripe" seeds before dispersal for periods ranging from a week or two, up to at least three years. After dispersal seeds of different species can be stored for periods of a few weeks, up to at least five years. For some species the lengths of periods of storage before and after dispersal, in relation to the seed germination period, appear to be complementary.

Seeds are prevented from germinating on their parents in fleshy fruit through the inhibitory effect of the fleshy tissues. In dry fruit, germination is prevented mainly by exclusion of water. After dispersal, seeds of many New Zealand forest species can germinate relatively quickly, in autumn and winter. Seeds of other species have their germination delayed for periods ranging from a few months to a few years by mechanisms which include requirements for moderately high temperature, or light, and immature embryos, thick, water-impervious seed coats, and biochemical blocking (i.e., dormancy *sensu stricto*).

Further research is needed on the demography of seed storage, the absolute longevity of seeds in storage, patterns of germination behaviour of various species and the mechanisms of germination delay.

KEYWORDS: pre-dispersal - post-dispersal - storage period - phenology - seedfall - germination delay.

INTRODUCTION

Seeds have three main functions. One is that through them parental genes may be reproduced and multiplied in new combinations, thus creating potential new generations of individual young plants. A second is that the formation of these relatively small, portable objects enables the new genotypes to be translocated for varying distances, whereas their parents are fixed in position. The third function is one of enabling the new genotypes to cope with environmental extremes or other inappropriate circumstances. This is achieved through the protection of the vital parts by covering tissues, and also by stasis, for a time, of processes which otherwise would lead to germination of the seeds. It is this third function which is the main focus of the present account. Aspects of the other two functions overlap with it, to some extent however.

One of the somewhat neglected implications of reproduction by seeds is their existence, after dispersal, as independent, genetically distinct entities. This is a fundamental fact of the population ecology of seed plants. Only obligate apomicts are exceptions to this rule, as they form clones through their genetically uniform seeds.

In many kinds of ecosystem it is recognized that viable seeds can be stored before they are in a position to germinate and give rise to new populations of juvenile plants. Descriptive and experimental studies on the physiology and ecology of the various related phenomena are summarized in Harper (1977), Roberts (1981), Bewley & Black (1985), Thompson (1987, 1992), Leck *et al.* (1989), Burrows (1989, 1994a, 1994b, 1994c), Fenner (1992, 1995) and Kigel & Galili (1995).

Harper (1957, 1977) popularized the term *seed bank*, in reference to populations of stored, viable seeds, likening them to funds being deposited in a bank account, held there for a time, then withdrawn. The term is widely used, especially in relation to seed storage in the soil after dispersal. Predispersal storage of seeds on their parents, is less well documented. In the light of the various ramifications of the natural seed storage phenomena the term *stored seeds* is preferred here as a general descriptor, meaning *populations of viable seeds, maintained naturally, before or after dispersal, and for various lengths of time, before germination.*

This account provides a brief summary of the general state of knowledge on seed storage in the context of plant reproductive sequences. It goes on to consider information available to date on seed storage in New Zealand native forests. At the same time a conceptual framework appropriate for further study is outlined.

Nomenclature of the plants noted in the tables and text is after Allan (1961), Moore & Edgar (1970) and Connor & Edgar (1987).

SEED STORAGE AND THE PLANT REPRODUCTIVE CYCLE

It is implicit hereafter, that though there are broad features common to all, the detailed structure, biochemistry and physiological and ecological behaviour of seeds of each species are uniquely different. Furthermore, in some species, individuals among seeds from one cohort, or even from a single parent, may exhibit more than one kind of behaviour in terms of seed storage, and emergence from it (Mott & Groves 1981).

During the continuous sequence of processes of plant reproduction, as outlined in Fig. 1, seed storage occurs in two distinct, but interlinked phases. The first is before dispersal, while seeds, though "ripe" (i.e., apparently mature and potentially capable of being independent), are often still protected to some degree by the presence around them of tissues derived from the parental ovary. The second is after dispersal, when the seeds are quite independent (though some retain investing maternal tissues).

The whole sequence begins with the fertilization of ovules and the subsequent development of fruit and seeds; there are parental influences both on the structures and sizes of seeds and on their physiology and metabolic functioning (Bewley & Black 1982, Gutterman 1992, Fenner 1995). The structures include the organs of the seed proper (embryonic root and shoot, cotyledons and endosperm, or other food storage tissue, enclosed by seed coats). Other structures that are often involved include organs derived from the ovary (e.g., enclosing and protective endocarp, and the pericarp which may function similarly but often is modified in a variety of ways to facilitate seed dispersal (Pool 1941, Mayer & Poljakoff-Mayber 1989)).

Structures and sizes of seeds or their parts depend on nutritional inputs from the parents. They may include photosynthetic products from the green, developing fruit.

Genetic effects in seeds arise, of course, from parental DNA inputs, but it is known, also, that there are biochemical impacts on differential germinability, resulting from phenotypic influences during the relatively long period of fruit and seed maturation. Some of these parentally-imposed effects are latent and programmed to become activated at some time in the future, usually after dispersal (Khan 1977, Gutterman 1992).

Seeds of some species are dispersed as soon as they are ripe. Others are maintained on their parents for varying lengths of time (Anon. 1948, Gill 1981, Willson 1992). Seeds in fleshy fruit and some dry fruit can be dispersed relatively quickly. By contrast, very long term storage on parents may occur in dry fruit. For example, in Australia, some species of *Banksia*, *Eucalyptus*, and *Hakea* bear rather woody fruit, containing live seeds, for many years. After a fire in which the parents may be killed, the resistant fruit open and release seeds, initiating the regeneration process (Gill 1981, Ashton & Willis 1982).

Dispersal results in many seeds reaching the ground. Some may germinate immediately, if their physiological state allows it and

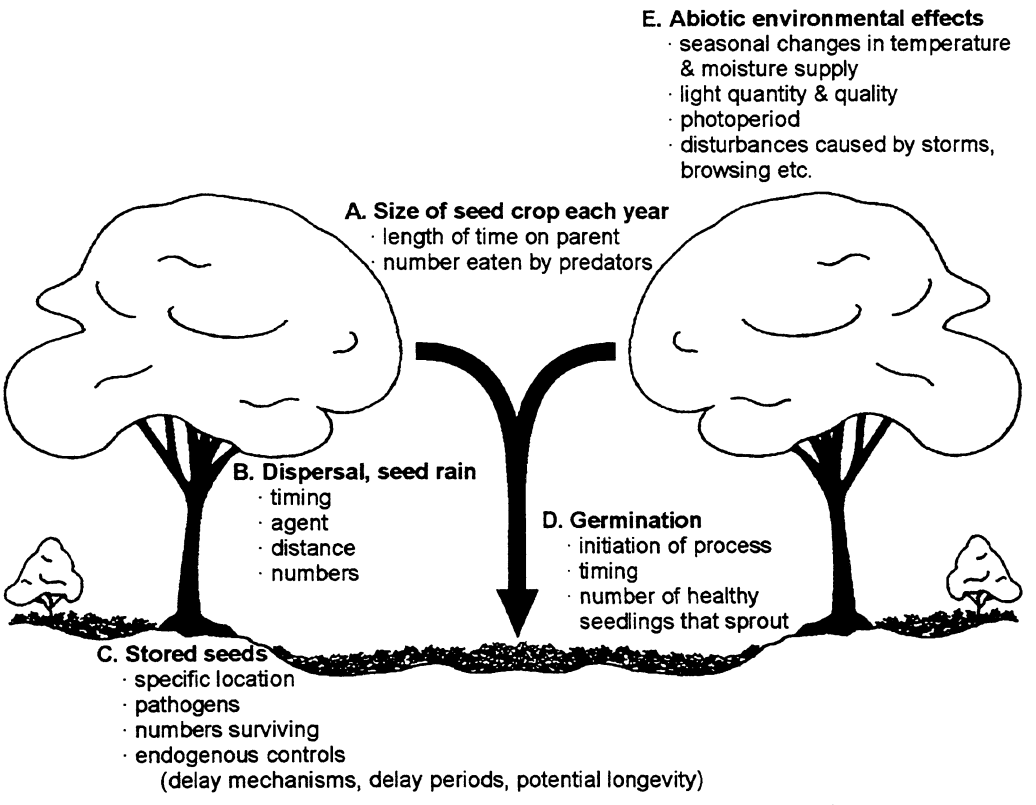

Figure 1. Diagram of important features of seed ecology of species in forests.

environmental conditions are suitable. Others go into storage for a variety of reasons that are outlined in more detail later. All stored seeds, including those on their parents, are vulnerable to the influences of pathogenic fungi, or predation, mainly by insects, birds and mammals (Louda 1989, Crawley 1992).

During the maturation process on their parents, seeds of many dry-fruited species undergo a natural desiccation process which renders them resistant to drought and cold. However, seeds in fleshy fruit do not dry out to the same degree. Also, seeds of some species that remain relatively moist (from dry, or fleshy fruit) can be killed by dry conditions of short duration (Bewley & Black 1982). To be stored safely they must be dispersed to wet sites, or at least be buried below the soil surface. Seeds not sensitive to drying may survive on the soil surface, or in the litter, humus, or deeper in the mineral soil.

Stored seeds remain in stasis (*i.e.*, are physiologically inactive) usually under the control of specific temperature, light and gaseous environmental conditions. Depending on the species and the circumstances, seeds may emerge from this quiescent state within a few months (often at the beginning of the next growing season, or after soil disturbance). However, some seeds may remain in stasis for periods of many years, or decades. For a few species, experimental evidence exists for survival of individuals from an initial cohort for up to a century (Egley 1989, Murdoch & Ellis 1992). Among the species with long-lived seeds are desert annuals (with very short-lived adults), many annual or biennial weeds of cultivated, or otherwise disturbed ground, and some perennial weeds which have seeds with very

thick, watertight coats. Similar research also reveals the fact that the maximum life span of seeds of each species is determinate, and uniquely long (Villiers 1973, Mott & Groves 1981, Murdoch & Ellis 1992).

Young plants often spring up in large numbers after soil disturbance. Seeds of many species that behave in this way must be unearthed before they can germinate. If there is no disturbance, ultimately the seeds will die.

GERMINATION DELAY

For seeds to remain in storage, before or after dispersal, their germination processes must be arrested. The various mechanisms for achieving this have been the subject of abundant research, often with the object of understanding how to get seeds to germinate, for some human purpose. The physiological and biochemical phenomena involved with germination delay often prove to be very complex and difficult to resolve (cf. Nikolaeva 1969, Grime & Jarvis 1976, Bewley & Black 1982, 1985, Baskin & Baskin 1985, Nikolaeva *et al.* 1985, Murdoch & Ellis 1992). The subject area is a maze of divergent views on appropriate concepts and terminology. As Burrows (1989) indicated, a generally-agreed and rational conceptual framework is badly needed. Table 1 outlines the apparent phenomena associated with germination delay.

The term *dormancy* has often been used, in a general sense, to describe any condition of arrested activity of seeds (cf. Harper (1957, 1977), who recognises several classes of dormancy). Recently the term has been used in a more specific sense to refer to the situation where, even though all external conditions are suitable, seeds will not germinate (cf. Murdoch & Ellis 1992). A case can be made for a restricted definition of dormancy, as it usually applies in plant physiology. Dormancy is the biochemical shutting down, or blocking, of metabolic processes, so that organs, or whole plants may outlast adverse environmental conditions. Release from the stasis is through environmental influences that signal the return of improved conditions (Larcher 1980). Other causes of delayed seed germination, *e.g.*, immature embryos, water impermeable-seed coats, or conditions that will not allow normal growth processes to operate, even though seeds are not dormant (insufficient oxygen, water, light, or inadequate temperature range) require other terms. Definitions are noted in Table 1 (cf. Burrows 1989, 1994a). At least, it is useful to be aware of the nature of the different causative factors when undertaking ecological analysis of germination delay and seed storage. They will be considered at greater length later.

In natural (or cultural) plant communities the species-specific behaviour of wild plant seeds that are in storage, or coming out of it, is linked with the kind of environmental background in which their evolution has taken place, allowing seeds to germinate at times when there is a strong likelihood of successful seedling establishment. For some species, it permits the germination risk to be spread over the seasons, or for several to many years. In temperate climates (with most of the literature being based on Northern Hemisphere examples) the winter cold period is very significant. A long episode of cold treatment overcomes dormancy and permits seeds to germinate (cf. Thompson & Grime 1979, Nikolaeva *et al.* 1985). In deserts, lack of water is the key factor. Specific amounts of precipitation are needed to release seeds from stasis (Mott & Groves 1981). Interactions with light quality, or composition of the gaseous environment are involved with dormancy and release from it in shaded forest environments and naturally- or human-disturbed habitats (Brenchley 1918, Roberts 1981, Bradbeer 1988, Garwood 1989, Parker & Kelly 1989). Similar influences have guided the evolution of the other germination delay mechanisms. Phylogenetic groups exhibit the same kinds of mechanism (e.g., thick seed coats in Papilionaceae; deep dormancy in Myoporaceae (Mott & Groves 1981, Burrows 1996b)).

SEED STORAGE IN NEW ZEALAND FORESTS

Research on topics relevant to seed storage in New Zealand indigenous forests has been of several kinds: (1) Phenological

Table 1. The range of germination delay behaviour in "ripe" seeds in natural conditions.

Patterns Observed	Likely Causes of Delay	Means by Which Delay is Overcome
I Pre-dispersal		
No delay - seeds germinate on parents (vivipary - relatively rare).		
Delay for varying periods depending on species and opportunities for dispersal.	**1. Inhibitors in fruit tissues.**	Removal of seeds from fruit by dehiscence, then leaching (dry fruit); or passage through frugivores (fleshy fruit).
	2. Environmental constraint - inability of desiccated seeds to become imbibed.	Dehiscence and dispersal.
	3. Immaturity, Physical constraint and **Primary Dormancy** (see 4., 6., 7. below).	
II Post-dispersal		
Delay for varying periods, depending on species and a variety of exogenous and endogenous influences.	4. **Immaturity** - embryos are not mature when seeds are dispersed.	Passage of time.
	5. **Environmental constraint** - unsuitable external conditions, most usually insufficient water or light, or oxygen; or the presence of high CO_2 concentrations, light of the wrong quality, unfavourable temperature regime, or waterlogged soil.	Change in the external conditions.
	6. **Physical constraint** - presence of thick seed coat, or combined seed coat and endocarp, which physically prevent ingress of water and oxygen and, in some cases may prevent expansion of the embryo.	Decay, or rupture of the coat/endocarp.
	7. **Dormancy** - biochemical blocking of metabolic processes. There may be numbers of underlying proximate effects. Dormancy may originate before seeds leave their parents (primary), or it can be imposed through impacts of environmental conditions on seeds after dispersal (secondary).	Influences of environmental effects which remove the blocks. They are specific for the seeds involved and may include one, or combinations of: periods of heating; prolonged chilling; fluctuating temperature of specific ranges; concentrations of chemicals (e.g., during fires); presence of ethylene; prolonged leaching (which removes inhibitors); changes in light quantity or quality.

Although seeds of many species can withstand dry conditions, some are unable to do so; to survive until germination they must remain continually moist. Other evident complexities of delayed germination include the presence of more than one of the delay mechanisms in seeds of particular species and variable manifestation of the intensity of action of delay mechanisms among seeds in a cohort. The actual behaviour of sets of seeds during the period of germination appears to reflect the responses of their germination delay (and release) mechanisms to changing environmental conditions. Among observed effects are: germination of all seeds in a set at the end of a period of delay; gradual germination of the seeds in a set, either in a regular, continuous pattern, or, with peaks in particular seasons, or conditions, or sporadically, over a long period.

References: Nikolaeva (1969), Bewley & Black (1982), Mayer & Poljakoff-Mayber (1989), Burrows (1994a) and Kigel & Galili (1995).

observations on fruit presence and seed removal in forest stands. This is a fair guide to pre-dispersal storage (cf. Beveridge 1973, Powlesland *et al.* 1985, Burrows 1994b, 1994c, O'Donnell & Dilks 1994, Leathwick 1984, Sem & Enright 1996) (Table 2). (2) Seed trapping in forest stands to obtain an appreciation of seed crops. The temporal range of seedfall in relation to season indicates, to some degree, the extent of seed storage on parents (Mirams 1957, Kirkland 1961, Franklin 1968, Beveridge 1973, Mohan *et al.* 1984a, 1984b, Allen 1987, Allen & Platt 1990, Burrows 1994b, Sem & Enright 1996). (3) Observations of the phenology of appearance of seedlings in forest stands. The timing of this in relation to seedfall is a guide to the period of seed storage in the soil, but it is not possible to discriminate between seedlings which may have been derived from cohorts of seeds that fell in more than one year (Kirkland 1961, Beveridge 1973, June & Ogden 1975, James & Franklin 1978, Ogden 1985). (4) Incubation of soil samples taken from forest stands to determine the composition and numbers of germinable seeds. Seedlings that appear may also be derived from more than one seed cohort (Herbert 1976, Ogden 1985, Enright & Cameron 1988, Partridge 1989, Sem & Enright 1995). (5) An important initiative, providing more information about the contributions made by seeds from one year's seedfall, was the 15 month study of Sem & Enright (1996). They caught seeds in lowland forest stands in trays of soil that were replaced at monthly intervals, then counted the seedlings which appeared. They also germinated seeds from soil which had been covered by the trays for 15 months. (6) Experiments on seed germination behaviour after treatments simulating conditions experienced after dispersal. Various species were investigated by authors noted in reviews by Fountain & Outred (1991), Bannister & Jameson (1994), Burrows (1994a) and by Clout & Tilley (1992), Ure (1994), Bannister *et al.* (1996), Ecroyd (1996), Ladley & Kelly (1996). See also Table 3. Tests involving burial of seeds were done by Beveridge (1973), Williams *et al.* (1996). Tests of seeds of many forest species in varied conditions (and indicating what delayed germination phenomena were evident) are reported in the reviews mentioned above and in Table 3.

PRE-DISPERSAL STORAGE

The phenological observations and seed trapping results show that almost all forest species store "ripe" seeds for a period before they are dispersed. Each species has a distinct fruiting period, which, for some may be synchronised over a relatively short period (one to three months), in a local area, while for others it is spread out over many months. Fruit maturation times also differ, some species requiring only a month or two, while, at the other extreme, some require more than a year. Most species bear ripe fruit in January-May, but in lowland forests, ripe fruit occur in overlapping sequence for different species through much of the year (Burrows 1994c, Leathwick 1984, Sem & Enright 1996, and Table 2).

Vivipary (germination of seeds before dispersal) is rare in woodlands. The only New Zealand species in which it always occurs, *Avicennia resinifera* (mangrove), lives in estuaries (Poole & Adams 1979). Its germinated seeds fall and float away before coming to rest on mud banks and taking root. Other species in which occasional viviparous germination has been observed are *Solanum laciniatum*, *Ripogonum scandens* and *Coprosma robusta* in which it occurred late in the fruiting season (C. J. Burrows, unpubl. data, Burrows 1993, 1996a); and *Corokia macrocarpa*, reported by Fountain & Outred (1991).

Examples of species with a range of pre-dispersal seed storage periods are noted in Table 2. Fleshy-fruited species may have their fruit eaten and seeds removed at any time after they ripen. It is noticeable that some spread the availability of fruit by continuous flowering over a period (e.g., *Fuchsia excorticata* (Delph & Lively 1985)); or by successive flowering episodes (e.g., *Melicytus ramiflorus* (Powlesland *et al.* 1985)). *Pseudopanax arboreus* and *Rhopalostylis sapida* individuals flower at different times over a very long period. Flowers and ripe fruit are often present on the same plant of

Table 2. The sequence of periods when ripe fruit occur on woody plants in North Westland-Buller forests. The timing of fruiting varies between plants, altitudes, aspects and years. This table reflects experience from direct observations in the interval 1995-1997. (C. J. Burrows unpubl. data and cf. O'Donnell & Dilks 1994). ■ main period with ripe fruit, □ a few ripe fruit present.

Species	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Fuchsia excorticata	■	■										■
Myrsine salicina	■	■									□	■
Coprosma grandifolia	■	■	■	■								□
Rhopalostylis sapida	■	■	■	■	■	■	□	□	□	□	□	□
Hedycarya arborea	□	□	■	■	■	□	□	□	□	□	□	□
Ripogonum scandens	■	■	■	■	■	■	■	■	□	□	□	□
Aristotelia serrata	■	■	■									
Coriaria arborea	■	■	■	□								
Macropiper excelsum	■	■	■	■								
Clematis paniculata	■	■	□									
Podocarpus totara	□	■	■	■								
Quintinia acutifolia	□	■	■									
Rubus australis		■	■	□	□							
Melicytus ramiflorus		■	■	■	■							
Prumnopitys taxifolia		■	■	□								
Solanum aviculare		■	■	□								
Dodonaea viscosa		■	■	■								
Coprosma robusta		■	■	■	■	■	□					
Pennantia corymbosa		■	■	■								
Pseudowintera colorata		■	■	■	■	■						
Coprosma lucida		■	■	■	■							
Griselinia littoralis		■	■	■	■							
Carpodetus serratus		■	■	■	■	□	□					
Dacrydium cupressinum		□	■	■	□	□						
Dacrycarpus dacrydioides		□	■	■	□							
Prumnopitys ferruginea		□	■	■	■	□						
Cordyline banksii		□	■	■	■	□						
Melicytus lanceolatus		□	■	■	□							
Myrsine australis		□	■	■	■	■	■	□	□	□	□	□
Weinmannia racemosa		□	■	■								
Pseudowintera axillaris			■	■	□							
Ascarina lucida			■	■	■	□	□	□				
Cordyline australis			■	■	■	■	□	□	□	□		
Schefflera digitata			■	■	■	■	■					
Pseudopanax crassifolius			■	■	■	■	■	□	□			
Pseudopanax edgerleyi			□	■	■	■	□					
Metrosideros robusta			□	■	■	□						
Pittosporum colensoi			□	■	■	■	□	□				
Metrosideros fulgens			□	■	■	■	■	□				
Griselinia lucida					■	■	■	□				
Freycinetia baueriana					■	■	■	□				
Metrosideros umbellata					■	■	■	■	□	□		
Metrosideros perforata						□	■	□				
Elaeocarpus dentatus						□	■	■	□			
Sophora microphylla [1]	■	■	■	■	■	■	■	■	■	■	■	■
Leptospermum scoparium [2]	■	■	■	■	■	■	■	■	■	■	■	■

[1] This species retains seeds in dry, indehiscent fruit for up to two years

[2] This species retains seeds in dry dehiscent fruit for up to at least three years

each of these species (Burrows 1994b, 1995d, 1996c). *Griselinia lucida* spreads the period of fruit availability by having only a few ripe fruit in its paniculate infructescences at any time over a two to three month period. *Myrsine salicina*, with clusters of fruit along the branches behaves similarly (C. J. Burrows, unpubl. data). The persistence of uneaten fruit may be a reflection of the relative paucity of fruit-eating birds in the forests today (cf. Burrows 1994c).

Maintenance of seed stores on dry-fruited species depends on other circumstances. Those species with dehiscent fruit (*e.g.*, *Parsonsia* spp., *Hebe* spp., *Kunzea*) often have characteristic, relatively brief, times for seed shedding. So do most species where the attachment of the whole fruit dehisces, allowing dispersal by wind (*e.g.*, *Olearia* spp., *Hoheria* spp., *Dodonaea*). Some other species have less determinate dispersal times. They depend on battering and abrasion during windy periods and also the gradual weakening, by decay, of the ties of the whole fruit or infructescence with the parent plant (*e.g.*, *Sophora microphylla*, *Plagianthus regius*) (C. J. Burrows unpubl. data, Burrows 1994b). Shedding of seeds from *Leptospermum* capsules can occur after very hot weather, or frost, or after a fire which burns the parent plant without consuming the rather woody fruit (Burrell 1965).

Though more or less continually moist, seeds in fleshy fruit do not germinate because their chemical environment is inhibitory (Partridge & Wilson 1990, Burrows 1995a, 1995b, 1995d). Bioassay tests show that presence of pericarp from a range of native forest species can prevent the germination of lettuce seeds (C. J. Burrows, unpubl. data). Dispersal, after consumption by, and passage through a bird, removes this inhibitory effect. Artificial removal of the pericarp, followed by soaking in water, does the same (Burrows 1995b). The nature of the inhibitors present in fleshy pericarps is uncertain. They might be water soluble polyphenolic/tannin compounds which are common in plants and known to inhibit the action of many enzymes (Kellam *et al.* 1992).

Failure of seeds to germinate in dry fruit can be caused by the presence of inhibitors (Burrows 1996c). Otherwise, tight enclosure of the embryo by seed coat and endocarp may prevent the ingress of oxygen. The presence of thick pericarp may have the same effect in fleshy fruit. Many intact dry fruit are impermeable to water. Even where, as in members of Asteraceae or *Clematis*, the clusters of fruit (achenes) are thoroughly wetted by rain they still dry out readily. A minimum amount and period of wetting is needed for seeds to become imbibed, so that the germination process can be activated (Bewley & Black 1982).

POST-DISPERSAL STORAGE

When seeds of many New Zealand forest plant species are separated from freshly-collected fruit (to simulate dispersal), then placed in moist, well-lit conditions, they germinate in a relatively short time (Table 3). This indicates that they are not primarily dormant (Table 1) and nor do they have other means of delaying germination.

Seeds of some other species germinate after longer initial delays. The causes and means of overcoming these delays are summarized in Table 1 and indicated for some individual species in Table 3. Each causal factor influences the seeds in different ways and this is likely to affect residence times of seeds in storage.

Those species which germinate in one to four months (mainly autumn and winter: March-July) (Table 3) do so when conditions are relatively moist, but cool. Lowland forest areas are frostless, or experience only very light frost (Garnier 1958). For species which germinate in six to nine months (late winter-spring-early summer: August-December) the new seedlings experience mild temperatures and moist conditions. Delays of 12-14 months (January-March) could be problematical for species in dry areas of the country because they are in the most drought-prone periods.

In many species with germination delayed for most seeds in the set, a few seeds sprout soon after dispersal, with a later episode of mass germination. Some species have a long tail of sporadic germination of a few seeds after the main peak.

Table 3. Examples of post-dispersal germination delay (and potential storage) for seeds from New Zealand forest species. Experimental conditions: fruit collected fresh, pericarps removed, seeds washed and placed in petri dishes, on filter paper, kept wet, in daylight , in an unheated, partly-shaded glasshouse, at University of Canterbury, Christchurch. Mean extreme temperatures: winter max. 13°C, min. 1°C; summer max. 22.3°C, min. 10.5°C

Species	Collection place, date	Period within which all seeds in a set germinated[Δ]	Likely causes of germination delay
Aristotelia serrata *	North Westland E Feb. 1996*	1 month	
Coriaria arborea	Marlborough Sounds M Jan. 1989; North Westland E Feb. 1994		
Dysoxylum spectabile °	North-west Nelson M May 1997		
Griselinia lucida *	North Westland E Jul. 1997		short delay as germination processes are initiated
Hedycarya arborea *	North Westland E Feb. 1994		
Knightia excelsa °	Marlborough Sounds M May 1997		
Melicytus ramiflorus *	Banks Peninsula M Feb. 1994; Marborough Sounds M Mar. 1996		
Metrosideros perforata °	North Westland L Aug. 1994		
Metrosideros robusta *	North Westland L Apr. 1996		
Alectryon excelsus *	Banks Peninsula E Feb. 1989	2 months	
Beilschmiedia tawa °	North Marlborough M Mar. 1996		
Coprosma robusta *	Christchurch E Oct. 1989		
Corynocarpus laevigatus	Kaikoura E Mar. 1994		
Fuchsia excorticata	North Westland M Jan. 1989; Banks Peninsula E Feb. 1996		
Griselinia littoralis *	Banks Peninsula M Mar. 1989		
Griselinia lucida *	North Westland M Aug. 1994		
Hedycarya arborea *	Kaikoura M Mar. 1996		

Table 3 (continued)

Species	Collection place, date	Period within which all seeds in a set germinated[Δ]	Likely causes of germination delay
Ileostylus micranthus °	Banks Peninsula M Jun. 1994	2 months	
Laurelia novae-zelandiae °	North-west Nelson M May 1997		
Macropiper excelsum	Marlborough Sounds M Dec. 1989; North Westland E Feb. 1994		as above, and for some species, (including those marked ♦)
Melicytus ramiflorus *	Christchurch E Feb. 1989		immaturity of embryos; environmental
Metrosideros robusta *	North Westland M May 1996		constraint (mainly low temperature)
Pennantia corymbosa *♦	Kaikoura M Mar. 1996		probably applies in some cases
Pittosporum eugenioides *♦	Christchurch E Jul. 1990		
Pseudopanax crassifolius	Banks Peninsula E Jul. 1990; L Jul. 1995		
Ripogonum scandens *	Kaikoura E Mar. 1994		
Tupeia antarctica °	Banks Peninsula M Jun. 1994		
Ascarina lucida *	North-west Nelson E Mar. 1997	3 months	
Coprosma grandifolia	North Westland M Mar. 1994; E Feb. 1996		
Coprosoma robusta *	Banks Peninsula L Feb. 1989		
Freycinetia baueriana *	North Westland E Sep. 1994		as above
Kunzea ericoides *	Banks Peninsula L Apr. 1996		
Schefflera digitata *	Banks Peninsula M Apr. 1989		
Solanum aviculare *	Buller E Feb. 1996		
Metrosideros robusta *	North Westland M May 1996		
Tetrapathaea tetrandra *	Christchurch L Apr. 1991		

Table 3 (continued)

Species	Collection place, date	Period within which all seeds in a set germinated[Δ]	Likely causes of germination delay
Coprosma robusta *	Christchurch M Mar. 1996	4 months	
Freycinetia baueriana *	North Westland M May 1994		
Geniostoma rupestre °	Marlborough Sounds E May 1996		
Griselinia littoralis *	Banks Peninsula E Apr. 1994		
Hoheria angustifolia °	Banks Peninsula M May 1994		
Kunzea ericoides *	Banks Peninsula L Apr. 1994		
Myrtus bullata °	North Marlborough E May 1996		
Myrtus obcordata *	Banks Peninsula L Apr. 1989		as above, constraint by low temperature is
Myrsine salicina *	North Westland E Jan. 1997		likely to affect most species in winter,
Pittosporum eugenioides *♦	Banks Peninsula M May 1996		secondary dormancy might effect some
Pittosporum tenuifolium *♦	Banks Peninsula L Apr. 1995; M May 1996		
Plagianthus regius *	Banks Peninsula L Apr. 1995; M May 1996		
Pseudopanax arboreus	Banks Peninsula M Apr. 1989; E Oct. 1989		
Schefflera digitata *	Banks Peninsula L May 1989		
Solanum aviculare *	Kaikoura M Mar. 1996		
Tetrapathaea tetrandra *	South Marlborough E May 1996		
Weinmannia racemosa °	North Westland L Apr. 1996		
Ascarina lucida *	North Westland M Mar. 1994	6 months	
Astelia fragrans *♦	North Westland M Mar. 1994		

Table 3 (continued)

Species	Collection place, date	Period within which all seeds in a set germinated[Δ]	Likely causes of germination delay
Carpodetus serratus *	South Buller E Jun. 1990	6 months	
Coprosma crassifolia °	Banks Peninsula L Feb. 1996		
Coprosma lucida *	Banks Peninsula M Feb. 1990		
Cordyline australis	North Westland M Mar. 1994; Christchurch M Mar. 1994		
Cordyline banksii °	Marlb. Sounds M Mar. 1996		
Corynocarpus laevigatus °	Kaikoura E Mar. 1994		
Freycinetia baueriana *	North Westland M May 1996		immaturity of embryos and constraint
Hedycarya arborea *	Banks Peninsula L Feb. 1991		by low temperature will have affected
Melicytus lanceolatus °	North Westland M Mar. 1994		some species; secondary dormancy
Muehlenbeckia australis *	Banks Peninsula L Feb. 1996		may have affected some; primary
Myrtus obcordata *	Banks Peninsula L May 1994		dormancy is likely to apply to some
Myrsine salicina *	North Westland E Dec. 1994		species (with release by a period of natural
Pennantia corymbosa *♦	Banks Peninsula E Apr. 1994		chilling
Pittosporum eugenioides *♦	Christchurch L Apr. 1995		
Pittosporum tenuifolium *♦	Banks Peninsula E May 1989		
Ripogonum scandens *	Banks Peninsula M Mar. 1991		
Schefflera digitata *	North Marlborough L Mar. 1996		
Solanum laciniatum	Banks Peninsula E Mar. 1994; L Feb. 1996		
Tetrapathaea tetrandra *	South Marlborough E May 1996		

Table 3 (continued)

Species	Collection place, date	Period within which all seeds in a set germinated[Δ]	Likely causes of germination delay
Alectryon excelsum *	Banks Peninsula E Mar. 1994	9 months	
Aristotelia serrata *	Kaikoura L Feb. 1994		
Carpodetus serratus *	North Westland M Mar. 1994		
Clematis foetida °	Banks Peninsula E Mar. 1996		
Coprosma lucida *	North Westland E Feb. 1994		
Dianella nigra *	North Westland M Mar. 1994		as above
Muehlenbeckia australis *	Banks Peninsula M Feb. 1990		
Pennantia corymbosa *♦	Banks Peninsula L Feb. 1989		
Pittosporum eugenioides *♦	Banks Peninsula M May 1996		
Plagianthus regius *	Banks Peninsula M Feb. 1990; Christchurch L Dec. 1994		
Rubus australis °	North Westland E Feb. 1996		
Streblus heterophyllus °	Christchurch M Feb. 1989		
Alseuosmia pusilla °	North Marlborough M Mar. 1994	12 months	primary dormancy
Dodonaea viscosa *	North Westland E Mar. 1996		physical constraint
Gahnia xanthocarpa °	North Westland M Mar. 1996		primary dormancy
Rhopalostylis sapida *♦	North Westland M Mar. 1996		immature embryo and low temperature constraint
Astelia fragrans *♦	Banks Peninsula M Feb. 1989	15 months	primary dormancy and immature embryo
Dianella nigra *	Buller E Feb. 1996		primary dormancy
Dodonaea viscosa *	Banks Peninsula M Mar. 1989		physical constraint

Table 3 (continued)

Species	Collection place, date	Period within which all seeds in a set germinated[Δ]	Likely causes of germination delay
Myrsine australis °	Banks Peninsula M Mar. 1994	15 months	primary dormancy
Pittosporum eugenioides *◆	Christchurch E Oct. 1989		immature embryo and possibly secondary dormancy
Rhopalostylis sapida *◆	Banks Peninsula L Jan. 1989		immature embryo and low temperature constraint
Pseudowintera colorata °◆	Banks Peninsula L Feb. 1989	18 months	immature embryo and primary dormancy
Parsonsia heterophylla °	Banks Peninsula M Apr. 1989	2 years	primary dormancy
Prumnopitys taxifolia °	Banks Peninsula M Apr. 1988		primary dormancy
Rubus cissoides °	Banks Peninsula E Jan. 1989		primary dormancy
Calystegia tuguriorum	Banks Peninsula E Mar. 1989	>5 years	physical constraint
Elaeocarpus dentatus °	North Westland L Aug. 1994	>3 years	primary dormancy
Melicope simplex °	Banks Peninsula L Feb. 1989	>3 years	primary dormancy
Myoporum laetum	Banks Peninsula L Jan. 1989	>2 years	primary dormancy
Myrsine divaricata °	Banks Peninsula L Feb. 1989	>4 years	primary dormancy
Sophora microphylla °	Banks Peninsula M Apr. 1994	>3 years	physical constraint
Urtica ferox °	Banks Peninsula E Jul. 1990	>2 years	primary dormancy

* Different sets of seeds of these species germinated over different periods. The periods selected for the table are arbitrary, but reflect the seasonal conditions to a considerable degree.

° Only one set of seeds of this species has been tested so far.

Δ Different species spread their germination in different ways. Some have an initial delay, then all germinate relatively rapidly. Others have sporadic germination of a few individuals, then a peak period when the rest germinate; numbers of species have a "tail" of a few individuals which germinate long after the main peak. A few species have seeds which germinate at a steady rate over a long period. For species which have periodic germination over several years there is usually a correlation of germination episodes with some environmental condition.

◆ E, M, L refer to the first, middle and last third of each month.

References: Burrows (1994d), Burrows (1995a, 1995b, 1995c, 1995d), Burrows (1996a, 1996b, 1996c, 1996d, 1996e, 1996f), C. J. Burrows, unpubl. data.

Evident from Table 3 are many cases of different behaviour (in terms of length of the germination period) for seeds of different provenances of the same species. In some instances (*e.g.*, *Hedycarya arborea*, *Coprosma robusta*, *Pittosporum eugenioides*) the differences appear to correlate with different periods of pre-dispersal storage (older seeds germinate more rapidly than younger ones) in other cases (*e.g.*, *Aristotelia serrata*) there is no such clear correlation. Other possible causes of the variable behaviour could include genotypic variation among different seed sets, or different phenotypic influences in different regions. Different pre-treatment or experimental conditions might also be involved, although attempts were made to obviate such effects. However the temperature regime in the glasshouse could not be controlled. Whatever the cause of the variability, it is evident that many species have flexible germination patterns, according to circumstances. This is probably an important feature of ecology of seeds in the forests.

The longest times for persistence, in conditions like those of natural storage, recorded so far for New Zealand species, are for hard-coated species such as *Prumnopitys ferruginea* (Preest 1963, Beveridge 1973, Clout & Tilley 1992); *Calystegia tuguriorum* and *Sophora microphylla* (Burrows 1996a, C. J. Burrows, unpubl. data).

Relatively few New Zealand forest species exhibit clear evidence for occurrence of primarily dormant seeds (where a metabolic block was imposed before they were dispersed). Some upland forest species appear to be in this category (Haase 1987) and other species are noted in Table 3. Examples from lowland forests are *Melicope simplex*, *Myoporum laetum*, *Myrsine divaricata* and *Urtica ferox* (Burrows 1996b). Some of the seeds of *Discaria toumatou* (matagouri), a shrubland plant, have germination delay resulting from both primary dormancy and a thick, water-tight seed coat. In other seeds of this species only the thick seed coat causes germination delay, and in others the seeds are not dormant and the seed coat allows ingress of water, so that they germinate readily (Keogh & Bannister 1992). This is the best known New Zealand example, so far, for varied behaviour of seeds from one cohort.

Research to unravel the mechanisms of biochemical blocking of seed germination requires experimentation using biochemical and molecular techniques. Virtually nothing has been done on this for New Zealand forest species. Applied research (McManus *et al.* 1994) suggests that proteinase inhibitors could play an important role. These also have other functions relevant to seed storage, as they serve as endogenous storage proteins and in protection against microbial and insect attack. A limited amount of physiological research in general has been done on the seeds of native forest species (cf. the reviews by Fountain & Outred 1991 and Bannister & Jameson 1994).

The post-dispersal studies on New Zealand seeds outlined so far indicate a potential for seeds of many species to be stored for periods of a few months, and for seeds of a relatively smaller number to be stored for longer periods, up to a year. Only a few have shown signs that they may be stored for longer (Table 3). These various indications of potential do not prove the longevity of seeds in natural storage, however.

Some other observations show that seeds are, or could be, stored in soil for a time: (1) The large numbers of seedlings of, *e.g.*, *Aristotelia serrata*, or *Melicytus lanceolatus* which sprout in disturbed forest areas (Burrows 1995b,1996f). (2) The large numbers of seedlings that appear in soil samples taken from forest. These include resident species of the sampled stand and invasive weedy species from nearby unforested areas (*e.g.*, Partridge 1989, Sem & Enright 1995, 1996). (3) The longevity of seeds kept in artificial storage (Preest 1963, Beveridge 1973, Platt 1987, Conner & Conner 1988).

Sem & Enright's (1996) study is the most important contribution so far, on the population dynamics of post-dispersal storage of seeds in New Zealand. It demonstrates that seeds falling at the study sites were derived from near and distant sources. Most seeds

fell in the period between early summer and late autumn. Seeds of 10 native species germinated while trays were still *in situ* in the field (i.e., within a month). Various other species germinated in a glasshouse within a few months and few native woody species were represented among seeds stored naturally in the soil for more than 15 months. There is, however, very little conclusive evidence from New Zealand of the actual mean and maximum residence time of seeds in the soil, nor of the flux of seeds into and out of storage.

CONCLUSIONS

Work done elsewhere indicates that stored seeds can have very complex behaviour and that they often play important roles in the population dynamics of plant communities (cf. Harper 1977, Silvertown 1982, 1988, Baskin & Baskin 1985, 1989, Fenner 1992, 1995, Egley 1995, Schupp & Fuentes 1995). However, except in Australia (cf. Noble & Slatyer 1980) there is little emphasis on pre-dispersal storage. This neglected aspect of seed ecology needs further study; there are interesting evolutionary connotations. For example Burrows (1994a) has suggested that interconnected fruit and seed properties of species in the New Zealand forest flora have developed, in part: (1) through affinities of many species with congeners in tropical and subtropical floras to the north and west; (2) through the importance of the mutualistic relationship with frugivorous birds, which disperse their seeds, and which inhabit the forests all year round.

As noted earlier, although seedfall for a majority of species is in summer-autumn-early winter in New Zealand forests, in the lowlands at least, an overlapping sequence of ripe fruit is present for most of the year. This sequential presentation of fruit (coordinated with a prior sequence of flowering, with the flowers providing nectar for at least some of the bird species, which are also both pollinators and seed dispersers) was thought by Burrows (1994c) to be the result of competitive selection among the plants for dispersers. Potentially long presence of fleshy fruit (and thus seed storage) is a striking feature of New Zealand forest ecology. Among the longest examples of pre-dispersal seed storage known in New Zealand, however, are dry-fruited species *Sophora microphylla* and *Leptospermum scoparium* (Table 2).

Inhibition of vivipary and prevention of decay of fruit pericarp while seeds are stored on their parents is a general feature for fleshy-fruited species everywhere (cf. Willson 1992, Burrows 1994c). It is not known why some New Zealand forest plants have very long fruit maturation periods (up to 18 months) (cf. Burrows 1994b).

Behavioural attributes of seeds of some New Zealand forest plants after dispersal have general features in common with seeds from elsewhere, especially evident from phylogenetic comparisons (*e.g.*, *Sophora* and *Chordospartium*, (Papilionaceae); *Urtica*, (Urticaceae); *Myoporum*, (Myoporaceae), Conner & Conner 1988, Burrows 1996b, C. J. Burrows, unpublished data). Some distinctive differences are evident, however, between the properties of seeds of New Zealand forest species and those of forests in the Northern Hemisphere temperate zone. There, many tree species have dry fruit and primarily dormant seeds which overwinter and germinate in spring or summer (Anon. 1948, Nikolaeva *et al.* 1985, Grime et al. 1988). In contrast, many seeds in New Zealand forests are not primarily dormant and are capable of germinating when they are dispersed, or soon after. This may be because the main period of seedfall, in later summer-autumn-early winter, coincides with the period of reliably wet soil conditions. Winter cold seems to have been less of an evolutionary imperative than summer drought, from the point of view of seed germination when conditions are suitable for seedling establishment. However, many species appear to be very flexible in the timing of germination of individuals among sets of seeds (Table 3). In parts of the country where rainfall is well spread through the year this will be advantageous.

The lack of primary dormancy in seeds of many New Zealand forest species (Table 3) was ascribed by Burrows (1994a) to the

relatively milder, oceanic climate here, not only at present, but throughout the Quaternary period, compared with places in the Northern Hemisphere, with its more severe continental climates. Other attributes of New Zealand forest plants (evergreenness of most angiosperms; lack of specialized bud coverings; lack of tolerance of the plants to low temperature) appear to arise from the same set of causes (cf. Burrows 1994a).

There is less evidence from dry-fruited species, but in contrast to the experience with dry-fruited species in the temperate Northern Hemisphere, most of which have deeply dormant seeds, at least some New Zealand species, in the genera *Metrosideros*, *Knightia*, *Kunzea*, *Laurelia* and *Pittosporum*, have seeds which are not primarily dormant (cf. Table 3).

From the accumulated experience on the role of seed storage in New Zealand forests, and taking into account the annual or longer-term behaviour of all species in the forests, it is possible to view pre- and post-dispersal seed storage as a temporal continuum. Some species store seeds very briefly and others do so for progressively greater lengths, up to at least four or five years. Classification of seed storage types (cf. Thompson 1992) is quite arbitrary in these circumstances. Hard-coated seeds like *Sophora microphylla* are likely to have the longest-lasting seed stores, but we know very little of the potential for relatively long-term storage of buried seeds of other species. Progress will be made by exploring the full range of behaviour that is possible for seeds of individual species.

What needs to be done now to gain a better understanding of the role of seed storage as one of the processes of New Zealand forest regeneration? The main requirements are: (1) Species-by-species demographic appraisal of the flux of seeds in forest systems from fertilization of ovules, to germination of all seeds from an initial cohort. This must be done by field studies following the fate of single seed cohorts from beginning to end (i.e., until the last seed has germinated, or died). (2) Long-term experimental studies of seed longevity in natural conditions. (3) Detailed experimentation on germination capabilities of seeds in a wide range of conditions, which are like those the seeds could experience in nature. These may need both field and laboratory tests. (4) Physiological, biochemical, and possibly molecular experimentation, exploring the many aspects of delayed germination, especially in its more cryptic expressions.

Several lifetimes of study are still needed on seed storage in New Zealand forests before we are really well-informed about this important phase of forest ecology.

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